THE RELATION OF BODY WEIGHT TO BODY SURFACE AREA IN MARINE FISHES

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In the course of attempting to establish a satisfactory basis for comparison of gill areas of certain marine fishes, considerable information about the body surface area has accumulated. Much has been written on the value of knowing the area of the body surface in metabolism studies and the difficulties in obtaining it. The formula most commonly used for determining surface area when the weight is known is $S = K\,w^{2/3}$, where S represents the area of surface, w is the body weight, and K is a constant for the particular species. Reported values for K have varied from less than 5 to more than 18 for different species. Benedict (1938), who has carefully reviewed at length his own work and that of others as it relates to metabolism and body surface, believes that with the exception of animals that tend to become spherical or greatly elongated, the value of K is in the neighborhood of 10. He gives 10 as "the best value of K" for 21 of 30 birds and mammals, with a range 9 (mouse, guinea pig) to 11.8 (macaque). He further points out, however, that there have been wide discrepancies in the determination of body surface area, even for the same species. More recently Zeuthen (1947) and Kleiber (1947) have also reviewed the subject and have called attention to variations and discrepancies reported in the literature. Kleiber (1947) recommends the use of the ¾ power of the weight as representative of metabolic size.

It is not the purpose here to enter into a discussion of metabolic rate, but rather to make available data concerning the relation of body weight to body surface in certain fishes.

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Methods of Obtaining Body Surface Area

A few trials quickly demonstrated that the use of 10 as a value for K in the formula $S = K\,w^{2/3}$, while giving approximately accurate determinations of body surface area in some fishes, produced wide deviations from experimentally obtained surface areas in other species. Measurements of body surface area were made directly on over 300 individual fish representing 39 species and 25 families. From these observations average values of K for the different species were determined.

Most data were obtained by following the method of Riess (1881), who determined the surface area of pike by drawing around the body, allowing for depth and omitting fins, and then calculating the area of the outline drawing. This procedure proved quite satisfactory for most of the fishes studied and particularly so for the greatly depressed or compressed species, such as flounders, butterfish, and cutlass fish. That greater difficulty was encountered in employing the method on odd-shaped fishes like the puffer, sea robin, and toadfish is reflected in the wider variations of individual determinations on these species.

A few attempts were made to determine the area of the removed integument of puffers but the skin stretched so readily that it was difficult to obtain consistent results and this method was abandoned.

Until some degree of proficiency was obtained in estimating the depth to allow in making outline drawings of the body of odd shaped fishes, the area of the outlines was checked by the more tedious and laborious method of covering the body with pieces of paper and obtaining the total area of the various pieces. The area of all outlines was secured by use of a planimeter.

RESULTS AND DISCUSSION

The values of K in the formula $S = K w^{2/3}$ for 39 species of fish are shown in Table I. It can be clearly seen that if the formula is to be used for the determination of body surface area in fishes, the value of K must be established for each species, or at least for each type of body plan. The more or less rotund species have low values for K while the greatly depressed and compressed species have high values.

TABLE I

Values of the constant K for marine fishes in the formula $S = Kw^{\frac{2}{3}}$, where S represents the area of body surface and w is the body weight

Family	Species of fish	No. of determinations	Weight in grams			Value of K		
			Max.	Min.	Ave.	Max.	Min.	Ave.
Clupeidae	Menhaden, *Brevoortia tyrannus*, adults	36	729	382	553	8.3	7.1	7.8
Clupeidae	Menhaden, small	10			19			8.7
Clupeidae	Thread herring, *Opisthonema oglinum*, small	4	46	40	43			8.7
Anguillidae	Common eel, *Anguilla rostrata*	4	562	94	345	11.8	10.7	11.3
Leptocephalidae	Conger eel, *Leptocephalus conger*	1	3519	3519	3519	10.2	10.2	10.2
Pleuronectidae	Fluke, *Paralichthys dentatus*	7	524	86	401	12.2	11.6	11.8
Pleuronectidae	Sand flounder, *Lophopsetta maculata*	1	395	395	395	15.3	15.3	15.3
Pleuronectidae	Winter flounder, *Pseudopleuronectes americanus*	2	745	723	734	14.7	14.6	14.6
Trichiuridae	Cutlass fish, *Trichiurus lepturus*	12	131	47	74	13.0	12.2	12.7
Scombridae	Common mackerel, *Scomber scombrus*	23	226	86	155	7.6	6.7	7.2
Scombridae	Bonito, *Sarda sarda*	2	2387	1998	2192	7.0	6.4	6.7
Scombridae	False albacore, *Gymnosarda alleterata*	1	2079	2079	2079	6.9	6.9	6.9
Scombridae	Spanish mackerel, *Scomberomorus maculatus*	9	483	39	234	8.9	7.6	8.3
Mugilidae	Jumping mullet, *Mugil cephalus*	5	250	132	165	8.8	7.5	8.0
Stromateidae	Harvest fish, *Peprilus alepidatus*	11	77	14	24	9.2	8.4	9.1
Stromateidae	Butterfish, *Poronotus triacanthus*	25	261	23	112	9.2	8.1	8.5
Carangidae	Big-eyed scad, *Selar crumenophthalmus*	3	55	52	53	7.2	6.7	7.0
Carangidae	Crevalle, *Caranx hippos*	10	155	80	120	8.8	7.6	8.0
Carangidae	Hard-tail, *Caranx crysos*	3	297	271	287	7.7	7.2	7.4
Centrolophidae	Rudderfish, *Palinurichthys perciformis*	6	294	106	199	7.8	7.1	7.5
Pomatomidae	Bluefish, *Pomatomus saltatrix*	4	1035	184	417	7.8	7.8	7.8
Coryphaenidae	Dolphin, *Coryphaena hippurus*, male	3	7033	2268	4258	9.7	9.2	9.4
Coryphaenidae	Dolphin, female	2	3289	165	1727	8.9	8.7	8.8
Moronidae	Striped bass, *Roccus lineatus*	4	2482	917	1648	8.8	7.5	8.0
Serranidae	Sea bass, *Centropristis striatus*	3	287	230	257	8.3	7.7	8.0
Pomadasidae	Pig fish, *Orthopristis chrysopterus*	1	60	60	60	7.9	7.9	7.9
Sparidae	Scup, *Stenotomus chrysops*	13	581	185	361	8.2	7.0	7.7
Sparidae	Pinfish, *Lagodon rhomboides*	4	58	49	53	8.0	7.0	7.5
Sparidae	Sheepshead, *Archosargus probatocephalus*	15	5216	54	1021	10.0	6.7	8.1
Scienidae	Spot, *Leiostomus xanthurus*	2	111	53	82	8.2	7.7	8.0
Scienidae	Croaker, *Micropogon undulatus*	4	62	40	48	8.1	8.0	8.0
Scienidae	Silver perch, *Bairdiella chrysura*	2	86	40	63	7.8	7.6	7.7
Otolithidae	Sea trout, *Cynoscion regalis*	6	1055	705	807	9.5	7.8	8.6
Ephippidae	Spadefish, *Chaetodipterus faber*	3	400	125	239	8.3	8.0	8.1
Triglidae	Brown sea robin, *Prionotus carolinus*	4	337	155	221	9.3	6.8	8.3
Triglidae	Red sea robin, *Prionotus strigatus*	10	1178	146	365	11.4	6.5	8.2
Labridae	Tautog, *Tautoga onitus*	6	1025	412	580	7.9	7.0	7.6
Tetraodontidae	Puffer, *Spheroides maculatus*	17	440	132	257	9.0	6.8	7.8
Diodontidae	Bur fish, *Chilomycterus schoepfi*	1	313	313	313	6.3	6.3	6.3
Batrachoididae	Toadfish, *Opansus tau*	58	776	15	233	11.5	6.3	8.9
Lophidae	Goosefish, *Lophius piscatorius*	2	4583	518	2551	9.5	8.8	9.2

Fusiform and moderately compressed species are intermediate in position. Of the species listed in Table I it is perhaps to be expected that the bur fish would have the lowest value for *K*, for this is a semi-rotund, short-bodied species. Highest values of *K* were recorded for the greatly depressed flounders. The value of *K* bears a relationship to habitat and taxonomic position only insofar as shape and relative weight are correlated with habitat and taxonomic position. The *K* value of fast-swimming pelagic fishes would not be at either extreme, for fast swimmers carry neither excess weight nor excess surface, as is often tolerated by bottom dwelling species.

It has been suggested that a puffer, when swelled to the maximum and thus practically spherical, would have the minimum value for *K*. This might be true if the fish filled up with water, but of course would not be true if puffed with air, for in the latter case the body surface would be increased without materially increasing the body weight. As a matter of curiosity an attempt was made to determine the surface area of a puffer both before and after swelling. As nearly as could be determined the area of the puffed surface was approximately double that of the unpuffed condition.

None of the fish used was taken during the breeding season and consequently the extra weight of ripe gonads was not a factor. With the exception of the dolphin no noticeable differences were detected between males and females. Dolphins exhibit marked sexual dimorphism and in this case males showed a significantly higher value for *K*. In other species males and females were lumped together.

Typical curves showing the relation of body surface area to body weight are presented in Figures 1 and 2 for the butterfish, mackerel, menhaden and toadfish. Comparison of the observed body surface area curves with area curves calculated on the basis $K = 10$ shows graphically that it is misleading to assume that the value of *K* is the same for all species. This is especially apparent for the larger mackerel (Fig. 1) and menhaden (Fig. 2), but is much less obvious for the toadfish (Fig. 2) where the observed value of K (8.9) more nearly approaches 10. There is also the possibility that the value of *K* is not the same for a species at all ages. Ten young menhaden averaging 19.3 grams in weight had a mean *K* value of 8.7 while for adult menhaden, weighing from 450 to 650 grams, the mean value for *K* was 7.8. The young menhaden exceeded the maximum value of *K* for adults. There is the pos-

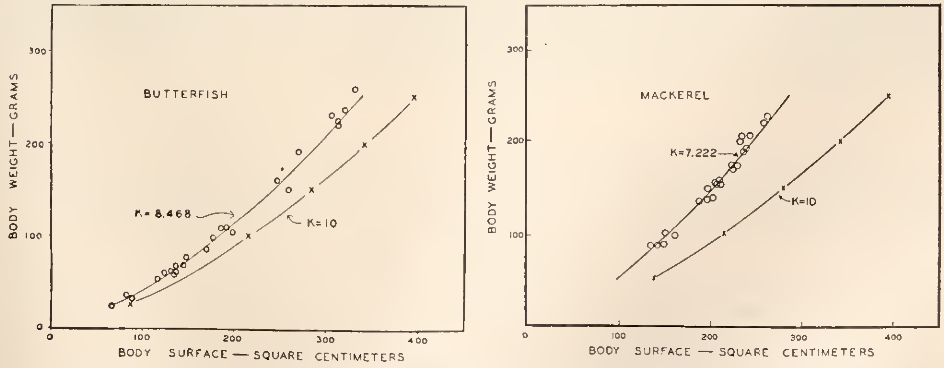

FIGURE 1. Relation of body surface area to body weight in butterfish (*Poronotus triacanthus*) and mackerel (*Scomber scombrus*). For comparison with observed values area computed on the basis $K = 10$ is also shown.

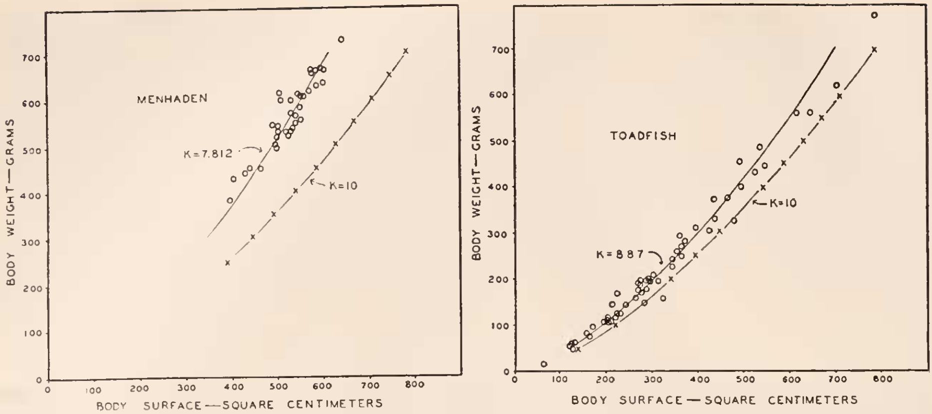

FIGURE 2. Relation of body surface area to body weight in menhaden (*Brevoortia tyrannus*) and toadfish (*Opsanus tau*). For comparison with observed values area computed on the basis $K = 10$ is also shown. The curves of Figure 2 are not on the same scale as those of Figure 1.

sibility in this case that the difference may be accounted for by error in the technique of determining the surface area of the small fish; but it seems more probable to assume that the difference in K value is due to differences in body proportions. Young menhaden are shorter bodied in relation to depth and are more compressed than adults. Four small thread herring of approximately the same shape as the small menhaden also showed higher values for K than did the adult menhaden.

In the surface area determinations on fishes the fins were excluded. Fish fins are modified in many ways and were they included as part of the body surface, the body area determinations would be misleading. For example, it was found experimentally that if the surface area of the pectoral fins of the red-winged sea robin was included as part of the body surface area, the value of K would rise to 17 instead of 8.2 when fins are omitted.

The magnitude of the deviations from the mean in the toadfish (Fig. 2) indicates the difficulty in accurately determining the surface area of some species. This raises the question of the value, in many cases of marine fishes, of expressing metabolism in terms of surface area as opposed to expressing it in terms of body weight, which can be so much more accurately and quickly determined.

SUMMARY

The value of K in the formula $S = K\,w^{2/3}$ has been determined for 39 species of marine teleosts representing 25 families. The values of K are in general higher for depressed and compressed species than for more streamlined fusiform fishes.

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